

Mate–location behavior in *Pereute* Herrich–Schäffer butterflies (Lepidoptera: Pieridae), with a review of male behavior at encounter sites in the subtribe Aporiina

MICHAEL F. BRABY^{1*} AND KENJI NISHIDA²

¹Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138–2902, USA; and Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia.

Present address: Biodiversity Conservation, Department of Natural Resources, Environment, the Arts and Sport, PO Box 496, Palmerston3, NT 0831, Australia

²Escuela de Biología, Universidad de Costa Rica, 2060 San José, Costa Rica

*michael.braby@nt.gov.au

Abstract. Male butterflies exploit a range of encounter sites, such as larval food resources, adult food resources and landmarks, to detect receptive females for mating. We present preliminary observations on behavior of males of *Pereute* and allied butterflies from South America which suggest that valley floors of ravines and gorges are used as non–resource–based encounter sites to locate mates. Males of *P. callinira* Staudinger, 1884, and *P. telthusa* (Hewitson, 1860) use these landmarks during the morning or around midday, are site tenacious (duration of visitation approx. 1–2 h), exhibit high site defense against conspecifics, and patrol a defined air space (territory): we hypothesize that these components comprise a mate–location tactic to locate receptive females. Similar behavior occurs in the closely related genera *Leodonta*, *Catantacta* and *Archonias*, although in *Catantacta* and *Archonias* males adopt a perching strategy while waiting at these and other landmarks. A review of available information on mate–location behavior in the Aporiina indicates a diverse array of tactics. Although there is little data on courtship of females and actual matings, non–resource–based sites (landmarks) are used most frequently as putative encounter sites, which as a rule are visited during the morning, and that patrolling behavior amongst males is widespread. Simple optimization of the component of waiting for receptive females in relation to a phylogenetic hypothesis for the Aporiina suggests that patrolling is ancestral and evolved in the common ancestor of the subtribe, whereas perching is derived and evolved relatively recently in the immediate common ancestor of *Catantacta* + (*Archonias* + *Charonias*). The selective forces that may have promoted this evolutionary switch in male behavior within the subtribe are briefly discussed.

Keywords: *Aporia*, butterfly behavior, *Cepora*, *Delias*, landmarks, *Leuciacta*, *Mylothris*, patrolling, phylogenetic history, territory.

INTRODUCTION

Butterflies utilize a range of encounter sites for mate–location, including larval food resources (pupation sites where females emerge, oviposition sites), adult food resources (foraging sites such as nectar of flowers), and non–resource–based

sites (landmarks) (Thornhill & Alcock, 1983). Rutowski (1991) summarized and reviewed the major components of male behavior at these encounter sites to detect receptive females. These components include visitation times (time of day), site tenacity (duration of visitation), site defense against conspecific males (degree of territoriality), and behavior whilst waiting for receptive females (patrolling or perching). Variation in these components, and hence differences in male–location tactics, is believed to be determined by the spatial and temporal distribution of receptive females (Emlen & Oring, 1977; Thornhill & Alcock, 1983). For the Pieridae, it was concluded that low site tenacity, no site defense and patrolling in this group of butterflies were the rule (Scott, 1974; Rutowski, 1991). However, this conclusion was based on limited data from the Coliadinae and two tribes

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within the Pierinae (Anthocharidini, Pierini); thus, data from a larger breadth of species within this group are likely to be informative. In this review we present preliminary observations on males of *Pereute* Herrich-Schäffer, 1867, from South America, namely *P. callinira* Staudinger, 1884 (Fig. 1) and *P. telthusa* (Hewitson, 1860) (Fig. 2), that are site tenacious, territorial and frequently employ patrolling flight behavior. Mate-location behavior in these species is then compared with related genera in the Aporiina reported elsewhere within the context of an evolutionary history of the subtribe.

MATE-LOCATION BEHAVIOR IN *PEREUTE*

Mate-location behavior among male *Pereute* butterflies was briefly described by DeVries (1987) and W. Haber (personal communication, 2000) for two species from Costa Rica in Central America: *P. charops* (Boisduval, 1836) and *P. cheops* Staudinger, 1884. Males of these butterflies typically select landmarks, which consist of forest edges, light gaps (i.e. prominent openings in the dense forest canopy where light reaches the understory) or, more usually, the crowns of the tallest trees in the forest. At these landmarks, individuals fly high in the forest canopy with a characteristic and conspicuous slow gliding or sailing flight with shallow wing beats. Each male occupies a defined air space by patrolling in long, circling flights to establish a territory, which is defended against rival males. Patrolling occurs from about mid-morning to midday and may last for several hours without pausing to settle.

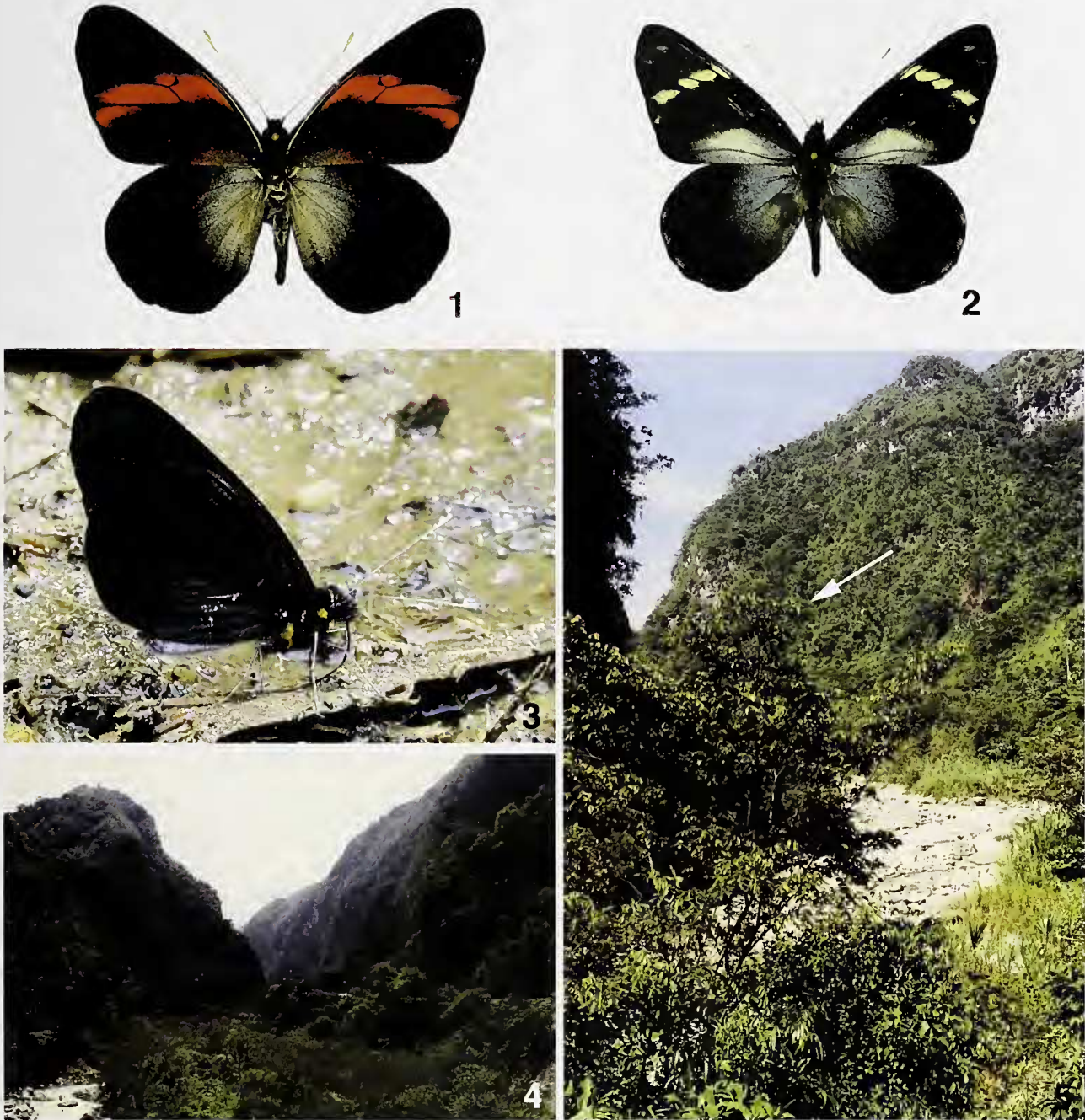
In late 2000, opportunistic observations were made in the montane tropical forests of the Chanchamayo district of Peru, South America. The Chanchamayo district lies in the upper Amazon basin on the eastern side of the Andes in steeply dissected country, and is a hotspot for butterfly biodiversity that is readily accessible from the capital Lima, 300 km further west. Five species of *Pereute* fly sympatrically in this area, namely: *P. callinira callinira*; *P. callinice numbalensis* Joicey & Talbot, 1928; *P. leucodrosime bellatrix* Fruhstorfer, 1907; *P. telthusa* and *P. charops peruviana* (Hopffer, 1878) (nomenclature of Lamas 2004). Behavioral observations were made chiefly on two of these species, *P. callinira* and *P. telthusa*, both of which are presumably involved in different mimicry complexes that include species of *Heliconius* (Nymphalidae: Heliconiinae) to which they resemble closely in wing pattern markings and flight behavior.

Field observations were made principally at two sites in the Chanchamayo district: (1) Cataratas de Agua Flor, Río Palca, 15 km SW of San Ramón (11°

10'S, 75°27'W; c. 1400 m a.s.l.); and (2) a tributary (creek) of Río Palca, 10 km SW of San Ramón (11°10'S, 75°24'W; c. 1300 m a.s.l.). Observations were conducted over eight days at the end of the dry season, from 7–10 and 14–17 November 2000. Sites were visited on alternate days, generally from 0800 h to 1600 h (i.e. each site was sampled four times). During 7–10 November, weather conditions were dry, sunny and hot with daytime temperatures reaching their seasonal maximum (c. 28°C). However, considerable rain fell during 11–13 November with the onset of the first pre-wet season storms, and weather conditions after this period were damp, overcast and cooler (c. 22°C), with only limited patches of sunlight around midday.

Pereute callinira Staudinger, 1884

In early November, prior to the pre-wet season storms, males of *Pereute callinira* (Fig. 1) were initially observed flying at the bottom of ravines where they established territories above the river or creek (Fig. 4). Up to six 'older' males (i.e. with slight to worn wing wear) occurred at each site. They typically selected a small sunlit area that included either the open air space above the water and canopy of nearby trees growing along the bank, or an open air space around the canopy of a small tree growing along the bank of the river (Fig. 5). These males flew generally at a height of 5–8 m from the water/ground level, although some males flew much higher, about 12–15 m above the water/ground level, if the flight space was located along steeper, narrower banks. Territories were about 10–20 m in diameter, and distributed linearly along the river or creek at intervals of 50 m or more. Males occupied these territories with a patrolling flight during which they rarely settled. The patrolling flight consisted of a slow sailing or gliding circling flight, with fore wings outstretched and oriented at angles between 135° and 180°, thereby exposing the conspicuous bright red median band, interspersed by a series of slow wing beats. When not interacting with other butterflies, males patrolled the same air space back and forth, but when conspecific males and other similar looking butterflies, for example, *Altinote* and *Abananote* (Nymphalidae: Heliconiinae: Acraeini), were detected they were intercepted and chased out of the flight space (territory). When chasing rival males the resident male often accelerated rapidly and flew at higher speeds. Patrolling behavior was limited to the mid-morning and usually lasted for 60–90 mins when conditions were cool but sunny. Males typically arrived around 0830–0930 h and then departed around 1010–1030 h, by which time



Figures 1–5. Study species and putative encounter sites near San Ramón, Chanchamayo district, Peru. 1. Male *Pereute callinira*. 2. Male *P. telthusa*. 3. Freshly emerged male *P. callinira* puddling. 4. Ravine showing bottom of valley floor (Río Palca) where encounter sites were established by male *Pereute* butterflies. 5. Encounter site of *P. callinira*; arrow indicates air space around canopy of tree growing along bank of Río Palca that was used by a particular male.

conditions were warmer. Although not confirmed by mark–release–recapture, resident males appeared to occupy the same territory on successive days during the observation period based on characteristic wing marks of individuals. Between 1010 h and 1100 h, nectar feeding among some of these males was noted

to occur, but from 1100 h to 1245 h (hottest part of the day) very few adults were encountered and none flew in open sunlit areas. The only males observed during midday were either settled on leaves of trees or shrubs in deep shade, or were flying very close to the ground along the bank of streams or over the surface of water

in shaded areas of the forest. When settled, males kept their wings closed, concealing the red median band and exposing only the inconspicuous black underside ground color of the hind wing. During the remainder of the afternoon (1245–1600 h) no males were observed flying at the bottom of ravines.

Following pre-wet season storms in mid-November a week after these initial observations were made, the temporal and to some extent spatial behavior of *P. callinira* changed dramatically. Rather than actively flying during the early morning, male activity was limited to a short period around midday, between 1140 h and 1400 h, when conditions were overcast but light levels were somewhat brighter than during the morning or late afternoon. Males also defended light gaps and small open areas in the mid canopy adjacent to the river, as well as open areas above the water.

At the second site, areas up to 400 m upslope from the creek were also surveyed for the presence of the butterfly. No males were detected flying on the steep slopes above the bottom of the valley.

In contrast to the territorial behavior described above, numerous 'younger' males (i.e. freshly emerged with no wing damage) of *P. callinira* (Fig. 3) were observed puddling from creek crossings in cool, shaded microhabitats. Males at these locations drunk water from moist sand and expelled water droplets from their anus, similar to that recorded for *Catantia* (DeVries 1987). Whilst drinking, the wings remained tightly closed so that the red median band of the forewing remained hidden beneath hind wing, making the butterflies very inconspicuous. Puddling behavior among these newly emerged males occurred throughout much of the day, from around 0830 h to 1600 h.

Pereute telthusa (Hewitson, 1860)

Males of *Pereute telthusa* (Fig. 2) were observed flying in sympatry with *P. callinira* at the second site. Prior to the pre-wet season storms, 'older' males (i.e. all with worn wing condition) of *P. telthusa* were observed in the gorge, with up to five individuals present, displaying patrolling behavior similar to that of *P. callinira*. They typically flew in an open sunny area above a track adjacent to the bank of the creek, about 5–6 m above ground level, with the territories of adjacent males separated by about 30 m. The patrolling flight consisted of a constant speed, flying back and forth over a defined area of about 10 m in length, during which they did not land or settle. The flight consisted of a slow gliding flight, with wings outstretched and open at an angle of approximately 135°. However, when a conspecific male entered the

flight space, the resident male flew more rapidly and aggressively chased the intruder from the area, and then returned to the territory to resume patrolling. The behavior lasted for no more than 1 h during the morning and generally occurred earlier in the day than that of *P. callinira*, from around 0820–0830 h to 0900–0930 h. Where the territory partly overlapped that of *P. callinira* (i.e. both species shared the same area in space and time), no interaction was observed, suggesting minimal interspecific competition between the two species.

Following the pre-wet season storms and cooler weather a week later, males were commonly observed patrolling light gaps and open areas in the mid canopy along and adjacent to the creek, but much later in the day, from 1140 h to 1400 h. Unlike *P. callinira*, males were not observed to puddle. However, like *P. callinira*, diurnal activity was restricted to the cooler hours of the day during warmer weather. Limited observations on the steep slopes above the bottom of the valley (up to 400 m upslope from the creek) failed to detect presence of the butterfly.

DISCUSSION

Older males of both *Pereute callinira* and *P. telthusa* were observed to use the air space above creeks and/or light gaps along banks of rivers at the bottom of valley floors of ravines and gorges. Further, their behavior at these sites suggests visitation times varied with temperature (mostly during the morning on hot days, or around midday on cooler days), with moderate site tenacity (duration of visitation approx. 1–2 h each day) and high site defense (resident males established territories and conspecifics were not tolerated), and that patrolling behavior was employed. Although no courtship or matings were observed in either species and no females were observed entering the flight space (territory) of males, we hypothesize that the pattern of male behavior exhibited by these species constitutes a mate-location tactic to locate receptive females and that the valley floors were used as a landmark-based encounter site (see Rutowski, 1991 for review of butterfly mating tactics). The components of this behavior in *P. callinira* and *P. telthusa* are broadly similar to that reported for *P. charops* and *P. cheops*, except the encounter sites differ in that *P. charops* and *P. cheops* utilize crowns of the tallest trees, forest edges or sometimes light gaps (DeVries, 1987; W. Haber, personal communication 2001) that are not necessarily located at the bottom of valleys in ravines and gorges. Salazar (2004) noted that adults of *P. leucodrosime* (Kollar, 1850) in Colombia are active in the morning during sunny

conditions and that they fly 4–7 m above the current of valleys and streams in the Andes, but he did not indicate if such activity comprised male mate–location behavior.

The failure to detect courtship or matings during the observation period is perhaps not surprising given that receptive females are generally very rare relative to searching males among insects, particularly among landmark–based mating systems (Thornhill & Alcock, 1983), and typically many hours are required to detect mating observations (e.g. in the pierid butterfly *Anthocharis pima* 20 h of observation yielded only one mating, while in other species more than 100 h yielded no mating) (Alcock, 1987). Nevertheless, it is puzzling that females of either species were not detected anywhere during the study period, and further observations are needed to ascertain their whereabouts. Presumably they remain in proximity of the breeding areas in search of suitable larval food plants or nectar sources, and that these resources either occur elsewhere in the valley or possibly further upslope from the valley floors. Observations made on males of both species suggest arrival schedules of receptive females may be thermally constrained, and that patrolling behavior is employed whilst waiting for these females, which presumably enter the encounter sites only briefly to mate before departing.

Rutowski (1991) concluded that for species that did not pupate on the larval food plant or feed on relatively small larval food plants, males should focus their mate–locating efforts on non–resource–based encounter sites such as landmarks in the environment. The early stages of *Pereute* are associated with mistletoes (Beccaloni *et al.*, 2008) and the larvae frequently pupate on the trunk of the host tree, usually some distance from the larval food plant (Braby & Nishida, 2010). Mistletoes are small aerial hemiparasitic shrubs in the plant order Santalales and have a patchy distribution in the landscape. These pupation habits and attributes of the larval food plant support Rutowski's generality that *Pereute* adults would be expected to use resources/sites other than mistletoes (i.e. the larval food plant) as encounter sites.

Among the non–resource–based encounter sites, insects have been recorded to utilize a wide–range of landmarks for mate–location. These landmarks are used primarily for mating, not for oviposition or adult feeding, and they include hilltops, gullies and riverbanks, prominent trees or bushes, forest clearings, open water, rock faces, patches of bare ground or places where microclimatic conditions enhance thermal requirements (Thornhill & Alcock, 1983). Hilltops are prominent, elevated landmarks

that are frequently used by males of butterflies and other insects as encounter sites to locate receptive females, which are promptly mated on arrival, and this mate–location behavior is characteristic of species that occur in low population density (rare or widely dispersed) (Shields, 1967; Scott, 1968; Alcock, 1987). In contrast, gullies and valley floors of ravines and gorges have been reported as landmarks for mate–location in only a few species. For example, males of the skipper butterflies *Ochlodes snowi* (Edwards, 1877) and *Hesperia viridis* (Edwards, 1883) use gullies for mate–location (Scott, 1973; 1974). In the former species, the males typically perch all day on stones, twigs or low vegetation at the bottom of narrow dry gullies whilst waiting for receptive females, but they do not engage in territorial defense (Scott, 1973). Similar behavior has been noted in males of the spider wasp *Pepsis thisbe* Lucas, 1894, except the encounter sites comprise dry desert washes (Alcock & Johnson, 1990). In this species, the males patrol throughout much of the day, with an apparent peak in activity during mid–morning (0800–1000 h); they also do not establish territories, but fly along routes which stretch for relatively long distances (Alcock & Johnson, 1990). In contrast, in *Pereute* and allied taxa (see below) the males of some species select small areas along valley floors of ravines and gorges in which they engage in territorial defense.

Further studies are needed to determine the extent to which valley floors are used as landmarks for mating. The above examples indicate that a range of insects utilize these landmarks as non–resource–based encounter sites, which suggests that there may be evolutionary convergence of a general landmark–based mating system among distantly related species.

Evolution of male behavior at encounter sites in the Aporiina

Rutowski (1991) concluded that the components of male behavior at encounter sites should be considered separately because they may evolve independently. To test this hypothesis of evolutionary independence, the various attributes of mate–location behavior of *Pereute* were compared with related genera in the *Catantacta* group and more broadly within the Aporiina in an evolutionary context based on review of accounts and reports in the literature and other data, and a published phylogeny for the subtribe (Braby *et al.*, 2007). *Pereute* belongs to a clade of eight genera from the New World, referred to as the *Catantacta* group, which includes *Melete* Swainson, [1831], *Leodonta* Butler, 1870, *Neophasia* Behr, 1869, *Eucheira*

Westwood, 1834, *Catantia* Butler, 1870, *Archonias* Hübner, [1831] and *Charonias* Röber, 1908. Species of *Melete*, *Pereute*, *Leodonta*, *Catantia* and *Archonias* occur in the Neotropical Region, are frequently sympatric, and all exploit similar larval food plants, that is, mistletoes (Braby & Nishida, 2010), whereas *Neophasia* and *Eucheira* occur in the Nearctic Region and the larvae feed on host trees that support mistletoes (Braby & Trueman, 2006). The *Catantia* group is closely related to *Delias* Hübner, [1819] and *Leuciactria* Rothschild & Jordan, 1905, from the Old World and *Aporia* Hübner, [1819] from the Palearctic Region and more distantly related to *Mylothris* Hübner, [1819] from the Afrotropical Region. These genera, together with *Cepora* Billberg, 1820, and *Prioneris* Wallace, 1867, predominantly from the Oriental Region, were placed in the subtribe Aporiina by Braby *et al.* (2006).

Published reports of specific male mate-location tactics and mating behavior in the Aporiina were found to be frequently anecdotal and for most genera several components of male behavior at encounter sites to detect receptive females were not reported. Moreover, courtship behavior and actual matings have rarely been recorded. However, the male flight behavior for most of these genera was well documented, and information on the components of type of encounter site, visitation times and behavior whilst waiting for receptive females (i.e. patrolling or perching) was usually reported.

Available information on mate-location behavior in the Aporiina is summarized at the generic level in Table 1. In general, non-resource-based sites (landmarks) appear to be used most frequently as encounter sites, which as a rule are visited during the morning, and that patrolling behavior amongst males is widespread in the subtribe. The types of landmark vary considerably and include tree canopies, light gaps, valley floors, banks of streams, hilltops and forest edges. The extent of site tenacity and level of site defense at these encounter sites are poorly known, although in the *Catantia* group these components appear to be of the order of one hour visitation during which a high degree of territoriality is displayed. Further quantitative data and more rigorous observations within the subtribe are needed to confirm these generalities and to test the assumption that the reported landmarks are indeed encounter sites at which courtship and mating takes place. This assumption holds true at least in *Delias* for which freshly emerged females and matings have been recorded at encounter sites in four hilltopping species (see below). Nevertheless, available data suggest that male mate-location tactics are diverse and vary within the group.

Within the *Catantia* group, the male behavior exhibited by *Pereuteis* is similar to that noted for *Leodonta* and to some extent *Neophasia*, *Eucheira* and *Melete*. In *Leodonta tellane* (Hewitson, 1860), males use riparian areas at the bottom of valleys and gorges as putative encounter sites, but breeding occurs some distance further upslope (Braby & Nishida, 2010). The males exhibit high territorial behavior by patrolling and defending the air space in prominent light gaps in the mid-canopy of riparian forest by flying rapidly in a small open area, typically at a height of about 5–8 m above the ground near the bank of a river or above water if the gap is located along a steep gully or ravine (Braby & Nishida, 2010). Such patrolling flights by individual males occurs during the morning (0930–1200 h) and may last for 1 h or more during which time they do not settle on foliage or attempt to leave the light gap. The resident male defends the light gap aggressively, chasing off rival males that enter the territory; if a resident male is removed from the light gap, another male soon enters its place and establishes a territory (Braby & Nishida, 2010). In *Neophasia*, Scott (1986) noted that the males of this genus patrol around the conifer larval host trees all day to seek females. Shapiro (2007, p. 102) described the mate-location behavior in *N. menapia* (C. & R. Felder, 1859) in slightly more detail, noting that the “Adults lek around the tops of pines and occasionally other trees, dropping to near the ground and then rising to near the top in a spiraling motion; they repeat the process again and again.” Similarly, males of the closely related monotypic genus *Eucheira* never perch, but establish leks around the tops of trees, which include the larval host tree (A. Shapiro and D.L.A. Underwood, personal communication, 2009). In *Melete*, the males of *M. lycimnia* (Cramer, 1777) patrol a defined area along the forest edge, flying 2–8 m above the ground during the morning under sunny conditions, with a slow fluttery flight (DeVries, 1987). Such behavior suggests *Melete* utilizes forest edges as encounter sites, although it is not known if they defend these sites and for how long.

In contrast, the males of several species of *Catantia* which have been studied, notably *C. teutila* (Doubleday, 1847), *C. sisamnis* (Fabricius, 1793), *C. hegemon* Godman & Salvin, 1889, and *C. flisa* (Herrich-Schäffer, 1858), typically perch with wings closed on foliage and other objects in the understorey, usually a few meters above the ground or at the tops of shrubs, along forest edges, in light gaps or riparian areas during the morning and vigorously defend small territories against conspecific males (DeVries, 1987; Braby & Nishida, 2010). Each site is occupied by a single male, and when an individual is removed from a

Table 1. Character states for various components of male mate-location tactics among the Aporiina. Question mark (?) denotes character state not recorded or there is uncertainty in state. For species which engage in site defense, the degree of territoriality was subjectively classified as either low (conspecific interaction among males noted) or high (conspecific males not tolerated by resident male).

Genus	Encounter site	Visitation time (time of day)	Site tenacity (duration of visitation)	Site defense (degree of territoriality)	Behavior whilst waiting for females	Reference
<i>Prioneris</i>	?	?	?	?	?	
<i>Cepora</i>	larval food plant	morning-midday	?	none	patrolling	M.F. Braby (unpublished data)
<i>Mylothris</i>	landmark (tree canopy)	?	?	low	patrolling	Larsen (1991; 2005), Henning <i>et al.</i> (1997)
<i>Aporia</i>	landmark (valley floor)	morning-afternoon	?	?	patrolling	Watanabe (1978), Wickman (1992)
<i>Delias</i>	landmark (hilltop)	morning-midday	?	low	patrolling	Common and Waterhouse (1981), Braby (2000 and unpublished data)
<i>Leuciactria</i>	landmark (tree canopy on ridges and summits)	morning-midday	?	low	patrolling	C.J. Müller (personal communication 2002)
<i>Melete</i>	landmark (forest edge)	morning	?	?	patrolling	DeVries (1987)
<i>Pereute</i>	landmark (valley floor, tree canopy, light gap, forest edge)	morning-midday	1-2h	high	patrolling	DeVries (1987); present paper
<i>Leodonta</i>	landmark (light gap in valley floor or along stream)	morning-midday	>1h	high	patrolling	Braby and Nishida (2010)
<i>Neophasia</i>	larval food plant (tree canopy)	morning-afternoon	?	?	patrolling	Scott (1986), Shapiro (2007)
<i>Eucheira</i>	larval food plant (tree canopy)	?	?	?	patrolling	A. Shapiro and D.L.A. Underwood (personal communication 2009)
<i>Catantacta</i>	landmark (light gap in forest or valley floor, forest edge)	morning	>1h	high	perching	DeVries (1987), Braby and Nishida (2010)
<i>Archonias</i>	landmark (light gap along stream)	early morning	1h	high	perching	DeVries (1987), Brown (1992), Braby and Nishida (2010)
<i>Charonias</i>	landmark (light gap)	morning	?	?	?	DeVries (1987)

particular site, another soon enters the site to take up residency, suggesting limited spatial availability and strong intraspecific competition for these landmarks. In *Archonias*, the males of both *A. tereas* (Godart, 1819) and *A. brassolis* (Fabricius, 1776) are most frequently observed in dense riparian forest along rivers and streams where the males establish and defend small territories early in the morning (DeVries, 1987; Brown, 1992; Braby & Nishida, 2010). They typically perch with wings closed on leaves or tall grass blades close to ground, usually a few meters above ground level, along the banks of rivers or narrow creeks and

display aggressive behavior towards conspecific males and other butterflies. Only limited information is available for the rare genus *Charonias*. The males of *C. eurytele* (Hewitson, [1853]) perch in and apparently patrol small light gaps about three meters above ground level during the morning (DeVries, 1987), but it is not known if they establish territories and engage in site defense.

Within the Aporiina, the behavior of male *Pereute* at encounter sites is remarkably similar to the flight behavior exhibited by males of *Delias*, especially species such as *D. harpalyce* (Donovan, 1805), *D.*

nigrina (Fabricius, 1775), *D. argenthona* (Fabricius, 1793) and *D. aganippe* (Donovan, 1805) from eastern Australia. In these species, which feed as larvae on mistletoes and allied plants (Braby, 2006), the encounter sites comprise prominent hilltops where the males congregate, often in large numbers, in the canopy to establish leks (Common & Waterhouse, 1981; Kitching, 1981; Braby, 2000). Although the encounter sites differ from those of the New World taxa, the behavior exhibited by males while waiting is similar in that they usually patrol with a soaring, fluttering flight with wings outstretched. In these four species of *Delias*, freshly emerged females and/or matings have also been recorded at hilltops (M.F. Braby, unpublished data). In *Aporia*, the males exhibit patrolling behavior to find mates (Watanabe, 1978; Wickman, 1992); in species such as *A. hippia* (Bremer, 1861) they typically fly along steep and narrow valleys and ravines throughout the day (Mitsuishi, 1988; Y. Nakamura, personal communication 2010). The flight behavior of *Mylothris*, in which the larvae also utilize mistletoes and related plants in the Santalales (Braby, 2005), is slow and measured (Larsen, 1991; 2005) and both sexes typically exhibit a floating flight (Henning *et al.*, 1997). Moreover, the males of several species, including *M. agathina* (Cramer, 1779), *M. trimenia* (Butler, 1869) and *M. rueppellii* (Koch, 1865), have been observed to flutter and glide for long periods around the canopy of tall trees, apparently supporting the larval food plants, where they establish territories during the warmer hours of the day and on subsequent days (Henning *et al.*, 1997).

The mate–location behavior of *Prioneris*, *Cepora* and *Leuciactria* is not reported in the literature, although unpublished observations for the last two mentioned genera suggest that males of both *Cepora* and *Leuciactria* do not perch but are obligate patrollers. In *Leuciactria olivei* Müller, 1999, from New Ireland, the males fly mainly during the morning, from around 0900 h to 1200 h, with activity ceasing after 1400 h, on the ridges and summits of mountains (C.J. Müller, personal communication 2002). They fly high in the canopy amongst the tops of the highest trees (c. 15 m above the ground) with a fast and direct flight, similar to that of *Delias totila* Heller, 1896, and *D. narses* Heller, 1896, and are highly aggressive, frequently chasing off conspecifics and other pierids. They rarely alight or descend from the treetops (C. J. Müller, personal communication 2002). Similarly, the males of *Cepora perimale* (Donovan, 1805) from Australia never perch (except when basking) during favorable weather, but fly rapidly within a few meters of the ground and appear to patrol the breeding areas in search of females on the larval food plant, *Capparis* spp., which

grow as vines or shrubs, from around 0900 h to 1300 h, or sometimes later without engaging in site defense (M. F. Braby, unpublished data). Males of *Prioneris* are well-known for their fast and rapid flight (e.g. Yata, 1985; Corbet & Pendlebury, 1992; Igarashi & Fukuda, 2000), but little is known of their courtship and mating behavior.

In terms of the evolution of the components of male mate–location behavior, data for most attributes in the Aporiina are too fragmentary to be analyzed in an evolutionary context, although it is apparent that there is a diverse array of tactics within the subtribe. However, an exception is the component of waiting for receptive females at encounter sites for which data are available for most genera (Table 1). In male mate–location behavior among butterflies, this component has been categorized into two broad tactics or character states: ‘patrolling’ and ‘perching’ (Scott, 1974; Rutowski, 1991; Wickman, 1992). In patrolling species, the males fly almost continuously and either wait or search for mates, whereas in perching species the males sit at characteristic sites and only leave the perch to court passing females or to intercept passing objects such as conspecific males. In some cases, males may adopt both strategies with patrolling employed as an alternative tactic to perching (Scott, 1974), but for the vast majority of species the males are either obligatory patrollers that never perch whilst waiting or they are perchers that typically sit and wait at encounter sites. Scott (2010) recently proposed a new system for describing this behavioral component, with the main objective of distinguishing between species which patrol and those which search whilst in flight; however, it remains to be seen if this system has broader utility and application compared with the present classification.

In the Aporiina, both ‘patrolling’ and ‘perching’ tactics for the component of male behavior whilst waiting at encounter sites for receptive females have been recorded. Most genera are patrollers, whereas perching is limited to *Catasticta* and *Archonias* (Table 1). In terms of character evolution, simple optimization of the two states in relation to a phylogenetic hypothesis for the Aporiina indicate that the most parsimonious sequence is that the patrolling strategy is an ancestral state that evolved in the common ancestor of the Aporiina, whereas the strategy of perching is a derived state that evolved relatively recently in the immediate common ancestor of *Catasticta* + (*Archonias* + *Charonias*) (Fig. 6).

The selective pressures that may have promoted this evolutionary switch in mating tactics from patrolling to perching in the Aporiina are unknown and, to our knowledge, it has not previously been

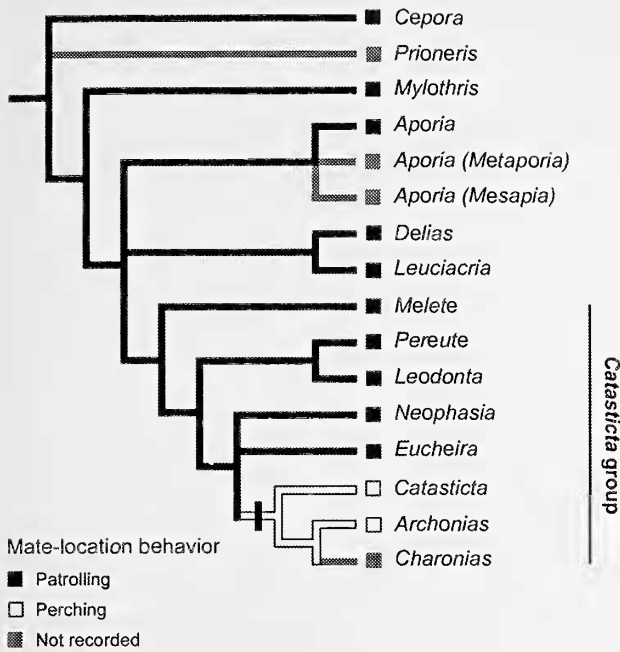


Figure 6. Phylogeny of the subtribe Aporiina (after Braby *et al.* 2007) showing evolution of mate–location tactics in relation to male behavior at encounter sites whilst waiting for receptive females. Vertical bar indicates character state change in male behavior from patrolling to perching.

reported. Several adaptive hypotheses have been proposed to explain the propensity of male butterflies to perch, including avoidance of predators such as birds (i.e. palatability hypothesis) (Wickman, 1992), lower ambient temperature (i.e. thermal constraint hypothesis), and lower male density (i.e. territory economics hypothesis) (Scott, 1974; Kemp, 2001). Alternatively, since patrolling and perching species in the *Catasticta* group appear to utilize different vertical air space, with patrolling species occupying larger areas further from the ground, the alternate tactics may be related to reinforcing reproductive isolation (i.e. reproductive–isolating mechanism hypothesis) (Alcock & Johnson, 1990) or to resource partitioning of microhabitats by courting males so that interference is minimized (i.e. interspecific competition hypothesis) (Scott, 1973). The latter hypothesis may be particularly relevant where the species occur sympatrically; for example, at San Ramón, males of *Pereute*, *Leodonta*, *Catasticta* and *Archonias* all occurred together at the two study sites.

Regardless of the ecological factors that may have shaped the evolution of different mate–location tactics in the Aporiina, the directional change from patrolling to perching is expected to have

profound effects on male butterfly design and flight performance due to male competition for mates (Wickman, 1992). The perching genera *Catasticta* and *Archonias* are predicted to have morphological traits associated with higher acceleration ability and speed, such as higher thorax/body mass ratio, higher wing loadings and higher aspect ratios (narrower wings) compared with obligatory patrolling genera *Pereute*, *Leodonta*, *Neophasia*, *Eucheira*, *Melete*, *Delias*, *Aporia*, *Mylothris* and *Cepora*.

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